

A Survey of Some Morphological Features of the Genus *Elaphoglossum* in Costa Rica

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The systematics of the over 400 species of *Elaphoglossum* (Aspidiaceae) is as little known or understood as any large genus of tropical ferns. Although the genus as a whole is pantropical, the majority of species are found in the Neotropics, an area in need of much botanical exploration. Endemism appears to be extremely common. A plethora of forms occupy similar habitats in the same region and many occur side by side on tree trunks and branches. Until much additional field work is done in the New World tropics, many of the species in the genus will remain undescribed.

Bell (1950; 1951a, b; 1955; 1956) initiated a series of morphological studies in the genus *Elaphoglossum* dealing with stelar structure, root and bud traces, and anatomy of the rhizome and frond. In these studies he made no attempt to correlate form with habitat. During the summer of 1967, I undertook a somewhat similar study in Costa Rica to add to our knowledge of morphology in the genus, as well as to correlate this with the basic habitat.

Plants were collected in seven geographical locations throughout Costa Rica: Peninsula de Osa (0–500 m elevation), San Ramón (1000 m), San Vito de Java (1100–1400 m), Volcán Poás (1800–2650 m), Volcán Barba (2200 m), Cerro de la Muerte (1200–3350 m), and Finca La Selva, south of Puerto Viejo (100 m). The habitats represented by these areas vary from Pacific and Atlantic lowland tropical wet forest to cloud forest, montane rain forest, and mossy elfin forest. Observations were made on the following characters: petiolar joints and swellings, pneumatophores, laminar scales, and sporangial features including paraphyses, number of indurated annular cells, and the presence or absence of chlorophyll in the sporangial stalk.

The data have been grouped according to plant habitat (epiphytic, epiphytic and terrestrial, terrestrial) and elevation (0–1000 m, lowland rain forest; 1000–2500 m, mid-elevation wet and

dry forest; and above 2500 m, high elevation wet forest). The climates of these areas are discussed by Scott (1966).

The data presented here represent only a summary of that collected. Mimeographed sheets with full results will be provided by the author on request. Voucher specimens have been deposited in the herbarium of the New York Botanical Garden. About 80 species were investigated, 70 in detail. Some of these are undescribed and the relationships of many others are in doubt.

TABLE I. HABITAT OF ELAPHOGLOSSUM BY ELEVATION

Elevation	Number of species and percent					
	<i>epi- phytic</i>	%	<i>terr. & epi.</i>	%	<i>terres- trial</i>	%
0-1000 m	13	93	0	0	1	7
1000-2500 m	29	76	0	0	9	24
above 2500 m	14	50	4	14	10	36
0-2500 m	42	81	0	0	10	19
Total	56	70	4	5	20	25

RESULTS

Habitat.—Of the 80 species of *Elaphoglossum* studied, 56 (70%) were epiphytic. There is a direct correlation between increasing elevation and frequency of terrestrial habit. At elevations below 1000 m, over 90% of the species were epiphytic, but above 2500 m only 50% occupied this habitat (*Table I*). In addition, those occupying both terrestrial and epiphytic habitats were found only at higher elevations.

Petiole Characters.—There is distinct variation in the petioles in *Elaphoglossum*. At the base of the petiole in the region where abscission occurs there may occur a joint or swelling. The joint refers to a point where there is a distinct color change where the petiole and phyllopodium join. This may or may not be accom-

panied by a slight swelling of the region (see Bell, 1955, *fig. 4.*). Of the 70 species investigated, 59 exhibited a distinct color change from petiole (usually green) to phyllopodium (usually dark brown or black). In 54 of these the joint was accompanied by swelling. Only five species possessed joints without swelling: *E. eximium* (Mett.) Christ, *E. aff. lindenii* (Bory) Moore, *E. muscosum* (Swartz) Moore, *Lloyd 4219*, and *Lloyd 4220*. The eleven species which were unjointed did not possess swellings. These results are similar to those of Bell (1955), who found a close association between the two characters with but only one exception.

Terrestrial species exhibited a greater frequency of joints and swellings than epiphytic (*Table II*), and those from middle elevations appeared to have a greater frequency with both structures than those from either lowland or highland areas (*Table IV*).

Pneumatophores.—Aerenchymatous flanges (or pneumatophores) are composed of loose, parenchymatous cells with large air spaces; they usually extend as a flange through the sclerified outer cortex of the phyllopodium. Bell (1955, *fig. 4*) recognized several types. They vary from narrow, lenticel-like lines extending from the base of the phyllopodium to the petiole to elaborate wing-like or phalloid structures of various sizes. They have been found in 92% of the species in Costa Rica, with the most frequent types being either a wavy, linear and somewhat fleshy tissue about 1–2 mm broad extending the length of the phyllopodium (Type C), found in 39% of the species, including *E. erinaceum* (Feé) Moore, *E. aff. hirtum* (Swartz) C. Chr., *E. hyalinum* Christ, *E. aff. lindenii* (Bory) Moore, *E. muscosum* (Swartz) Moore, and *E. aff. tectum* (Humb. & Bonpl.) Moore; or a phalloid structure about 2–4 mm long and 1–2 mm wide, arising from and restricted to the region near the base of the phyllopodium (Type G). This type of pneumatophore is always associated with densely scaly rhizomes and is found in 18% of the species, including *E. conspersum* Christ, *E. herminieri* (Bory & Feé) Moore, *E. longifolium* (Jacq.) J. Smith, *E. revolvens* (Kunze) C. Chr., and *E. squamipes* (Hook.) Moore. The most common type of pneumatophore (C) occurs in 46% of the epiphytic species and only 15% of the terrestrial. Type G is

TABLE II. PERCENT OF SPECIES WITH CHARACTERISTICS IN
RELATION TO EPIPHYTIC, TERRESTRIAL AND EPIPHYTIC,
AND TERRESTRIAL HABITAT

<i>Character</i>	<i>Habitat</i>			<i>Mean</i>
	<i>epiphytic</i>	<i>terr. & epi.</i>	<i>terrestrial</i>	
Swelling	78	50	85	71
Jointed	80	75	95	80
Pneumatophore ^a				
Type A	4	0	20	9
B	12	0	5	8
C	46	75	15	39
D	4	0	15	7
E	6	0	10	7
F	13	0	10	11
G	15	25	25	18
Scales: adaxial				
Glabrous	50	25	60	52
Type A (<i>fig. 8-1</i>) ^b	2	0	0	1
B (<i>fig. 7</i>)	14	25	5	12
C (<i>fig. 8-7</i>)	14	25	30	19
D (<i>fig. 8-10</i>)	7	0	0	4
E (<i>fig. 8-11</i>)	13	25	5	12
Coverage:				
Under 10%	80	25	80	77
10-40%	15	75	15	19
Over 40%	5	0	5	4
Scales: abaxial				
Glabrous	14	0	20	15
Type A	2	0	0	1
B	9	0	10	9
C	52	25	50	50
D	7	50	5	9
E	16	25	15	16
Coverage:				
Under 10%	80	50	85	79
10-40%	2	0	0	2
Over 40%	18	50	15	19
Paraphyses:				
present	68	0	43	56
absent	32	0	57	44

found in 15 % of epiphytic forms and 25 % of terrestrial. There is a trend to lack of pneumatophore in terrestrial species, with 20 % lacking this structure. In the epiphytes only 4 % were lacking it.

Mature pneumatophores were frequently observed on the rhizome in areas of leaf primordia. In many instances as the petiole developed, the tissues of the pneumatophore appeared to fuse with those of the petiole. The function of the structure is unknown, although Troll (1933) believed that it was for aeration in areas of high metabolic rate, especially where aeration was restricted, such as croziers with heavy mucilage. This substance has not been found in *Elaphoglossum*, however.

Although Type C is the most common type of pneumatophore, at elevations above 2500 m there is a sharp increase in number of species without pneumatophores and with Type G (*Table IV*).

Laminar Scales.—The structure of scales and hairs on the frond varies from simple or capitate glandular hairs to peltate scales. The variation in structure found in plants from Costa Rica is similar to that found by Bell (1955, *fig. 8*) for plants from other areas of the world. The most common scale type was laminate, attached at the base with cordate or lobed basal wings (Bell, *fig. 8-7*). In only six species did scale types differ on the adaxial and abaxial surfaces: *E. auripilum* Christ, *E. aff. hirtum* (Swartz) C. Chr., *E. muscosum* (Swartz) Moore, *E. revolvens* (Kunze) C. Chr., *E. aff. tectum* (Humb. & Bonpl.) Moore, and *Lloyd 4220*. In *E. auripilum* and *E. aff. tectum* the more complex scale type was found on the adaxial surfaces.

Over half of the 70 species examined in detail possessed no scales at all on the adaxial surface. Of those with scales, 77 % had a coverage of less than 10 % and only 4 % had a coverage of greater than 40 % (*Table II*). Sixty percent of the terrestrial species and 50 % of the epiphytic were glabrous. In most instances the trends

^a Pneumatophore types: A. None. B. Lenticel line extending from the base of the phyllopodium into the petiole; no flange. C. Lenticel line present with slight flange near the base. D. No lenticel line; slight flange present at base of phyllopodium. E. No lenticel line; definite flange present. F. No lenticel line; enlarged flange. G. No lenticel line; club-shaped flange.

^b Figures of the various types are from Bell (1955).

present on the adaxial surface were similar to those found on the abaxial surface. On the abaxial surface, however, scale density was greater, with about 18% of the species having over 40% coverage.

Elevation apparently has no profound effect on either scale type or density. From the data given in *Table III*, there appears to be only a slight trend toward more scaliness on the abaxial

TABLE III. NUMBER OF SPECIES OF EACH SCALE TYPE
IN RELATION TO ELEVATION

<i>Elevation</i>	<i>Scale type^a</i>						<i>%</i>
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>	<i>Glabrous</i>	<i>Glabrous</i>
Adaxial Surface							
0-1000 m	0	0	0	0	1	3	61 ^b
1000-2500 m	1	5	8	1	4	17	47
Above 2500 m	0	3	5	2	3	15	54
Abaxial Surface							
0-1000 m	0	0	3	0	1	0	26 ^b
1000-2500 m	1	4	18	2	5	7	19
Above 2500 m	0	2	14	4	5	3	10

^a See Table II for scale types and references to illustrations in Bell, 1955.

^b Based on 13 species, 4 of which were analyzed as to type.

surfaces at higher elevations. However, this trend appears to be reversed on the adaxial surface.

Paraphyses.—Copeland (1947, p. 119) stated that paraphyses are wanting in *Elaphoglossum*. However, recent studies by Anderson and Crosby (1966) indicate the presence of paraphyses in some Hawaiian species. A survey of fertile fronds in Costa Rican material indicates that 56% have paraphyses. In most cases the paraphyses are short, uniseriate, multicellular branches arising from the upper portion of the sporangial stalk near the base of the sporangium. In a few cases they arise from the receptacle

(*Lloyd 4268*) or from both the receptacle and the sporangial stalk (*Lloyd 4284*). They are usually glandular at maturity. Paraphyses occur in 68% of epiphytic species and only 43% of terrestrial (*Table II*).

TABLE IV. PERCENT OF SPECIES WITH CHARACTERISTICS
IN RELATION TO ELEVATION

<i>Character</i>	0-1000 <i>m</i>	1000-2500 <i>m</i>	2500-above
Swelling Present	75	84	68
Jointed	75	90	79
Pneumatophore:			
Type A ^a	25	5	11
B	0	13	4
C	0	45	36
D	0	8	7
E	25	5	7
F	25	13	7
G	25	11	28
Paraphyses Present ^b	100	54	61
No. species investigated	4	38	28

^a See Table II for description of types.

^b Based on percent of taxa with fertile fronds.

Asexual Reproduction.—Vegetative reproduction is infrequent in most ferns and rare in *Elaphoglossum*. In the Costa Rican material it was found in only one species, *E. undulatum* (Willd.) Moore (*Lloyd 4177*). Plants of *E. undulatum* occur in very wet secondary forest near San Ramón and regularly produce asexual buds from the terminal portion of the midvein of the frond. This species was usually epiphytic, normally between 0.5 and 1 meter above ground level, with pendent fronds which frequently came in contact with the soil. Buds and new plantlets were observed on mature fronds, increasing in size as the parent fronds aged. As the parent fronds degenerate, the new plantlets formed terrestrial colonies at the base of the tree.

Other Sporangial Features.—Sporangia tend to arise in numerous, circular sori below the veins. As the fertile fronds mature, these sori merge together and become acrostichoid. The number of indurated annular cells of the sporangia vary from 10 to 15, with 12 being the most frequent. Chlorophyll is present in the sporangial stalk in about one-third of the species.

DISCUSSION

The most obvious trend found in this study in *Elaphoglossum* is toward the terrestrial habitat with increasing elevation. In lowland rain forest, 93 % of the species were epiphytic. In highland wet forest (above 2500 m) only 50 % of the species were epiphytic. This trend is frequent in other groups of plants, including Bryophyta, Bromeliaceae, and Orchidaceae. At lower elevations species are either terrestrial or epiphytic, but not both. At upper elevations, particularly in exposed habitats, this distinction breaks down. The cause of this phenomenon is only vaguely known. Wet cloud forest, with its somewhat stunted trees, has altered the terrestrial habitat and permits normally epiphytic species to grow. This may be due to increased humus, mosses, water and light. At lower elevations the available moisture in the soil is greater than that on the trees, but here other factors, such as lack of light or available substrate, must control plant distribution. There is little evidence to indicate whether the terrestrial habitat is less extreme than the epiphytic, although it is apparent that the former may provide the more suitable habitat during dry periods in those areas with a marked wet-dry climate. Terrestrial habitats also provide greater protection from drying winds. Some terrestrial habitats, especially those of disturbed areas along roadsides where there is no protective cover, appear to have more extreme conditions. Species of *Elaphoglossum* that occur in these habitats have coriaceous fronds, a feature that Lloyd (1965) found to be associated with xeric environments in *Polypodium*.

There are certain characters correlated with either epiphytic or terrestrial habitat. These are:

<i>Epiphytic</i>	<i>Terrestrial</i>
Non-jointed	Jointed
Non-swelling	Swelling
Type C pneumatophore	Type G pneumatophore
Pneumatophores present	Pneumatophores absent
Scaly	Glabrous
Type B, C, & E scales (adaxial surface)	Type C scales (adaxial surface)
Paraphysate	Non-paraphysate

The strongest of these trends is toward the absence of paraphyses in terrestrial plants. In addition, there is a slight increase in the frequency of paraphyses with higher elevations, although the number of terrestrial species also increases. If paraphyses evolved as protective structures against desiccation of young sporangia, epiphytic plants more exposed to changing conditions would be expected to show a higher frequency of presence. This might also be true of plants in more extreme situations at higher elevations.

Bell (1955) found a close association between the joint and the presence of pneumatophores, although he believed that they were probably independently controlled genetically. The function of the pneumatophore is unknown. The function of the joint may be as a mechanism for shedding leaves, as in *Oleandra*. Holttum (1966) believed that this was an adaptation to the epiphytic habit. However, in *Elaphoglossum*, terrestrial plants show a higher frequency with joints than do epiphytes. Species at higher elevations also possess this structure less frequently.

The trends in scaliness are of uncertain significance. Plants with both glabrous and densely scaly fronds occur side by side in many different habitats. Christ (1899) believed that species at higher elevations tended to have densely scaly fronds and those at lower elevations glabrous fronds. My results indicate that the adaxial surface of the frond is less densely scaly at higher elevations than at mid-elevations. However, on the abaxial surface

scale density increases with elevation. Over 50% of the species from elevations above 2500 m had glabrous fronds or fronds with less than ten percent of the surface covered by scales.

It is obvious from this study that the relationship between the characters investigated and the habitat is complex. The wide diversity in structure may be due to maintenance of much of the diversification through time since the origin of the genus in a stable, continuously tropical habitat (Bell, 1956), and in fact, there may be no correlation with habitat for many of the features I studied. Further studies are needed, however, before definite conclusions can be reached as to the evolution of the various features and their relationship to the environment.

Use of Characters for Taxonomic Purposes.—Many of the features elaborated in this study appear to be useful for taxonomic delineation of species. Of particular importance are scale type, pneumatophores, presence or absence of a joint and phyllopodium, and presence and type of paraphyses. Bell (1955) found that the scale types are constant in any one species. This may be true of the other features, although large numbers of individuals of each species have not been investigated. Nearly all 70 species can be distinguished using a combination of these characters.

ACKNOWLEDGEMENTS

Much of this work was done while I was involved in a course on the biology of tropical pteridophytes, sponsored by the Organization for Tropical Studies. I am indebted to that organization and to the University of Costa Rica for providing funds and facilities while in Costa Rica. I am also indebted to Drs. W. H. Wagner, Jr., J. T. Mickel, D. B. Lellinger, A. M. Evans, and C. V. Morton for their helpful criticisms and comments during the study. Specimen identification was done by Drs. Mickel and Lellinger.

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News and Notes

FERN FORAY PARTICIPANTS should write for details to Miss Lois Carlson, Matthaei Botanical Garden, University of Michigan, Ann Arbor, Mich. 48105 if they have not already done so.

MRS. CHARLES BITTINGER, who was instrumental in developing the Fern Valley at the National Arboretum in Washington, D. C. during the 1950's, died in Washington on April 24 at the age of 95. She had been active in garden club activities in the Washington area for many years, and had received honors from the Garden Club of America. She was also interested in music and the other arts, and was a member of the Women Geographers, an arm of the Explorer's Club. She described the establishment and growth of the Fern Valley in a well illustrated article several years ago (*Amer. Fern J.* **51**: 161–173, 1961).